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BEHAVIOURAL RESPONSES TO SEASONAL VARIATIONS
OF AUTOECOLOGICAL PARAMETERS IN POPULATIONS
OF *SPELEOMANTES STRINATII* (AELLEN, 1958)
AND *S. AMBROSII* (LANZA, 1955)

(AMPHIBIA, PLETHODONTIDAE)

INTRODUCTION

Plethodontid salamanders are characterized by specific and distinctive morphological and physiological features, which confine them to very humid environments and relatively mild temperatures. However, they are able to respond to adverse environmental conditions (low relative humidity and extreme temperatures), remaining in suitable underground refuges until conditions improve (JAEGER 1980; BOBKA *et alii* 1981; FEDER 1983; HAIRSTON 1987). The species belonging to *Speleomantes*, which is the only genus of the Plethodontid family present in Europe, are general predators which were long considered to live exclusively in caves, whereas it has been ascertained that, given favourable conditions in terms of humidity and temperature, they can also be found in epigean environments, especially at night (LANZA 1946, 1999; STEFANI 1969; SALVIDIO 1991; LANZA *et alii* 1995).

The ecological and ethological responses given by *Speleomantes* populations to the changes of various environmental parameters have been the object of a few studies (LANZA *et alii* 1995; LANZA 1999) until, recently, a number of research papers have been published

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on the ecology of *Speleomantes* populations in Italy (this volume). These studies have provided interesting data regarding population size and structure and their relationships with environmental parameters. There is still some doubt, however, on the interpretation of the behavioural responses of individuals found in hypogean or epigean habitat, and on their possible seasonal movements between these two habitats. We, therefore, decided to investigate the seasonal ecological responses given by two populations of *S. strinatii* and two of *S. ambrosii ambrosii* (FORTI *et alii* 1997; CIMMARUTA *et alii* 1999).

MATERIALS AND METHODS

The researches were carried out in two sites populated by *S. strinatii* (Aellen, 1958) (sites 1 and 2) and two by *S. a. ambrosii* (Lanza, 1955) (sites 3 and 4). Sites were selected from populations already genetically characterized to ensure their correct taxonomic identification (NASCETTI *et alii* 1996; FORTI *et alii* 1998). They were situated in easily accessible caves, with external rock walls that could also be inspected without difficulty at night. The location and main characteristics of the sites are shown in tab. 1. Environmental parameters of the four sites were regularly analysed from 1990 to 1997 and measurements of temperature (T) and relative humidity (H), both inside (T_i , H_i) and outside (T_e , H_e) the caves, were taken. Inside the cave, measurements were taken approximately 6-7 metres from the entrance. The availability of potential preys was also quantified by recording the number of invertebrates inside the cave either by direct count or, where they were present at high density, through estimation based on a 1m² surface sample area.

The surface activity of *Speleomantes* (i.e., specimens active on walls and floor either inside either outside the cave: N_i and N_e , respectively) was estimated by direct count. Outside the caves, counting was carried out over a standard sample area of approximately 200 m² around the entrance, starting two hours after sunset, when salamanders activity is potentially highest. On the basis of its total length each individual was classified in one of three age classes, according to DURAND (1970, 1973): I) newborns: juvenile individuals from hatching to 5-6 months (from 26 to 38 mm); II) juvenes: juvenile individuals from 6 months to three years (42 to 75 mm); III)

adults: individuals older than three years (length greater than 75 mm).

The correlation between the various parameters was extrapolated using the Pearson method.

Table 1 - Geographical location and environmental description of the four studied sites.

Site	Coordinates	Height (m)	Vegetation type	Canopy extent	Geological substrate	Cave length	Entrance width (m)
<i>S. strinatii</i>							
Site n. 1 (Rocca Roncallo)	44°20'16"N 09°28'01"E	435	mesophilous	100%	limestone	35	1,5 x 1,5
Site n. 2 (Baracchino)	44°16'25"N 09°33'23"E	760	mesophilous	100%	ophiolites	10,5	2,1 x 1,1
<i>S. ambrosii</i>							
Site n. 3 (Monte S. Nicolao)	44°15'37"N 09°30'43"E	720	termophilous	30%	ophiolites	11	3,6 x 1,2
Site n. 4 (Cassana)	44°12'37"N 09°51'27"E	180	mesophilous	100%	limestone	14,5	0,7 x 0,6

RESULTS

1) Seasonal activity in epigean and hypogean habitats.

The observations carried out evidenced that all the four studied populations showed activity both inside and outside the hypogean part of the site. Moreover, there was a marked seasonal variation in the number of individuals found inside and outside the cave at each site, correlated to environmental parameters (figs. 1-4 and tab. 2).

In the *S. strinatii* population from site 1, surface activity of the individuals outside the cave (N_e) was higher in spring and autumn, the lowest degree of activity being observed in the summer (fig. 1a). Surface activity in the cave (N_i) was highest in summer and lowest in winter, with intermediate levels in spring and autumn (fig. 1a). At this site, the internal temperature (T_i) of the cave was higher during the summer but was relatively constant with respect to the outside temperature (T_e) which varied more greatly (fig. 1b). The relative humidity within the cave (H_i) was high and steady whilst the outside value (H_e) was variable, with summer minimums being directly related to rainfall in the area (fig. 1c).

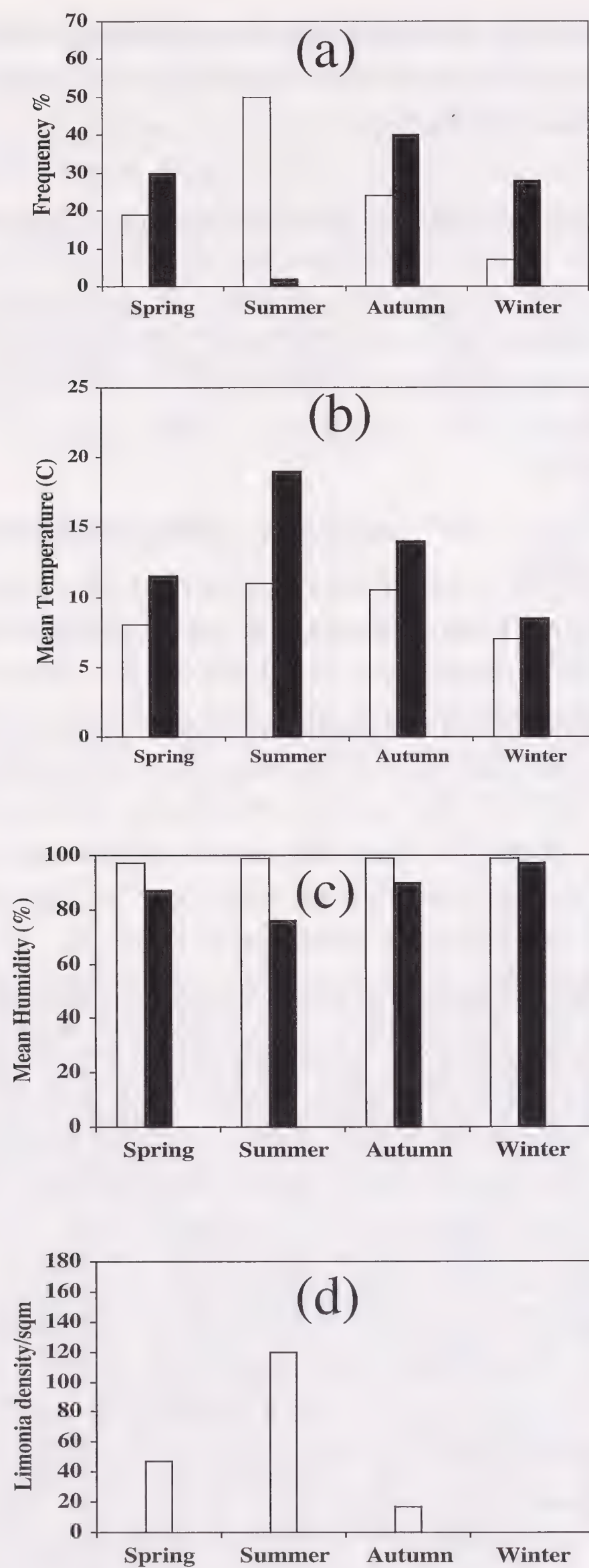


Fig. 1 - Mean values averaged per season of the following parameters recorded inside (white) and outside (black) the cave from *S. strinatii* site 1: a) number of specimens (N_i and N_e); b) temperature (T_i , T_e); c) humidity (H_i , H_e); d) density of *Limonia* flies (N_{lim}).

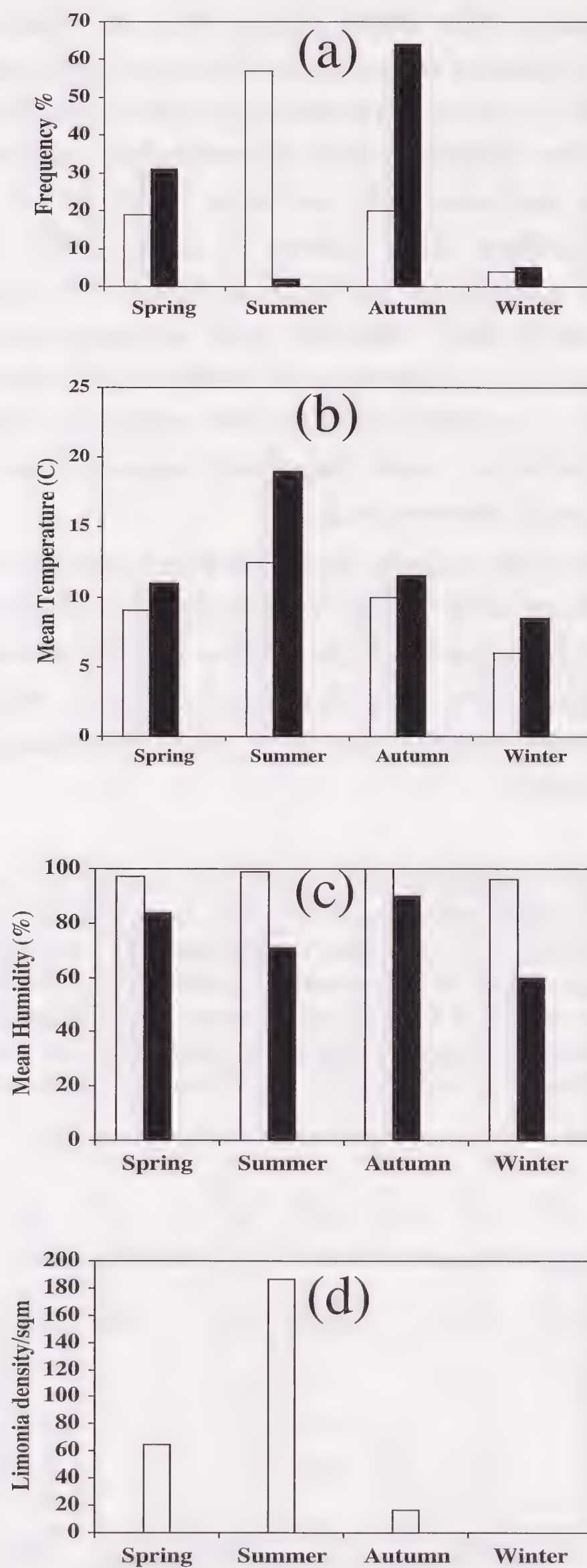


Fig. 2 - Mean values averaged per season of the following parameters recorded inside (white) and outside (black) the cave from *S. strinatii* site 2: a) number of specimens (N_i , N_e); b) temperature (T_i , T_e); c) humidity (H_i , H_e); d) density of *Limonia* flies (N_{lim}).

Moreover, inside the cave there was a marked presence in summer of flies (*Limonia nubeculosa* Meigen) (fig. 1d). These insects spend the summer in caves and other humid retreats and are actively preyed upon by the plethodontid salamanders, as can be seen from analysis of faeces and stomach contents (pers. obs.). As reported in tab. 2 in this population the number of individuals found inside the cave (N_i) showed a positive correlation with the internal and external temperature and flies' density and a negative correlation with external humidity. The number of individuals found outside the cave (N_e) showed a positive correlation with the external humidity and negative correlation with the flies' density and with both the internal and external temperature.

A similar seasonal pattern has also been observed in the *S. strinatii* population from site 2 (fig. 2, tab. 2). The number of individuals found within the cave (N_i) correlates positively with the internal and external temperature and the flies' density, whilst the number of individuals found outside the cave (N_e) correlates positively with the external humidity.

Table 2 - Correlation coefficients (r) between the number of *Speleomantes* observations inside (N_i) and outside (N_e) the cave and the environmental parameters recorded (T_i : internal temperature; T_e : external temperature; H_i : internal humidity; H_e : external humidity; N_{lim} : density of *Limonia* flies within the caves); + (-) positive (negative) significant correlation $P < 0.05$; ++ (--) positive (negative) highly significant correlation $P < 0.01$; +++ (---) positive (negative) very highly significant correlation $P < 0.001$.

Site	N_i					N_e				
	vs T_i	vs T_e	vs H_i	vs H_e	vs N_{lim}	vs T_i	vs T_e	vs H_i	vs H_e	vs N_{lim}
n. 1 <i>S. strinatii</i>	++	+++		-	+++	--	---		+++	--
	0.58	0.68		-0.42	0.67	-0.58	-0.67		0.81	-0.56
n. 2 <i>S. strinatii</i>	++	+			+				+++	
	0.68	0.62			0.66				0.78	
n. 3 <i>S. ambrosii</i>		-	++	+++					+++	
		-0.34	0.52	0.64					0.78	
n. 4 <i>S. ambrosii</i>	+++	+++			+++		-		+++	--
	0.62	0.541			0.564		-0.35		0.70	-0.440

In the *S. ambrosii* population from site 3 (fig. 3) we found, instead, a surface activity of the individuals in the cave (N_i) which

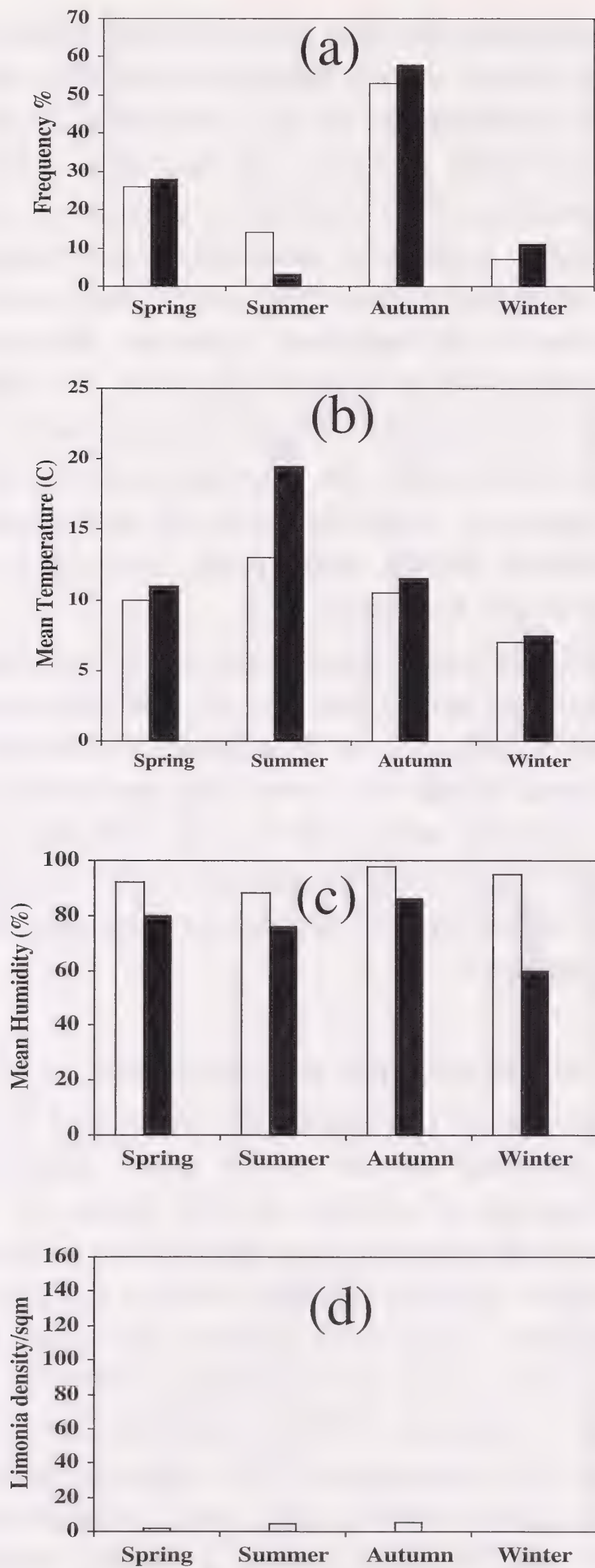


Fig. 3 - Mean values averaged per season of the following parameters recorded inside (white) and outside (black) the cave from *S. ambrosii* site 3: a) number of specimens (N_i and N_e); b) temperature (T_i , T_e); c) humidity (H_i , H_e); d) density of *Limonia* flies (N_{lim}).

is similar to that outside the cave (N_e), usually higher in spring and autumn, with the lowest values falling in summer (fig. 3a). At this site, the internal temperature of the cave (T_i) in summer reaches values higher than those recorded at the other studied sites, and the external temperature (T_e) undergoes greater variations (fig. 3b). The relative humidity inside the cave (H_i) is not constant and varies according to the external values (H_e) with lower values in summer (fig. 3c). Furthermore, in summer, *Limonia* flies are not present inside the cave with high numbers (fig. 3d). As shown in tab. 2, in this population the number of individuals found inside the cave (N_i) correlates positively with the internal and external humidity. It also correlates negatively with the external temperature, whilst the number of individuals found outside the cave (N_e) correlates positively with the external humidity.

In the *S. ambrosii* population from site 4 we found a seasonal pattern similar to that noted for the *S. strinati* populations from sites 1 and 2 (fig. 4, tab. 2). In this latter population, the number of individuals found inside the cave (N_i) correlates positively with the internal and external temperature and with the density of flies, whilst the number found outside the cave (N_e) correlates positively with the external humidity and negatively with the flies density and the external temperature.

2) Observations on the dispersal of individuals.

Individual movements between the cave and the outside environments were recorded at site 2 for three subsequent years by individual toe-clipping of adults, in the frame of an experiment of artificial syntopy (CIMMARUTA *et alii* 1999). A female recaptured for three consecutive seasons provided direct evidence of individuals moving repeatedly inside and outside the cave. First caught in the central part of the cave in November 1992, it was recaptured and marked again in January 1993 outside the cave, some 25 metres from the entrance. In September 1993, this specimen was captured once again in the central part of the cave. Salamanders move from inside to outside also in short times: a young specimen observed outside the cave, about 5m from the cave entrance, was inside the cave the following night. More generally, considerable movements were observed for several specimens, as far as 80m from the cave

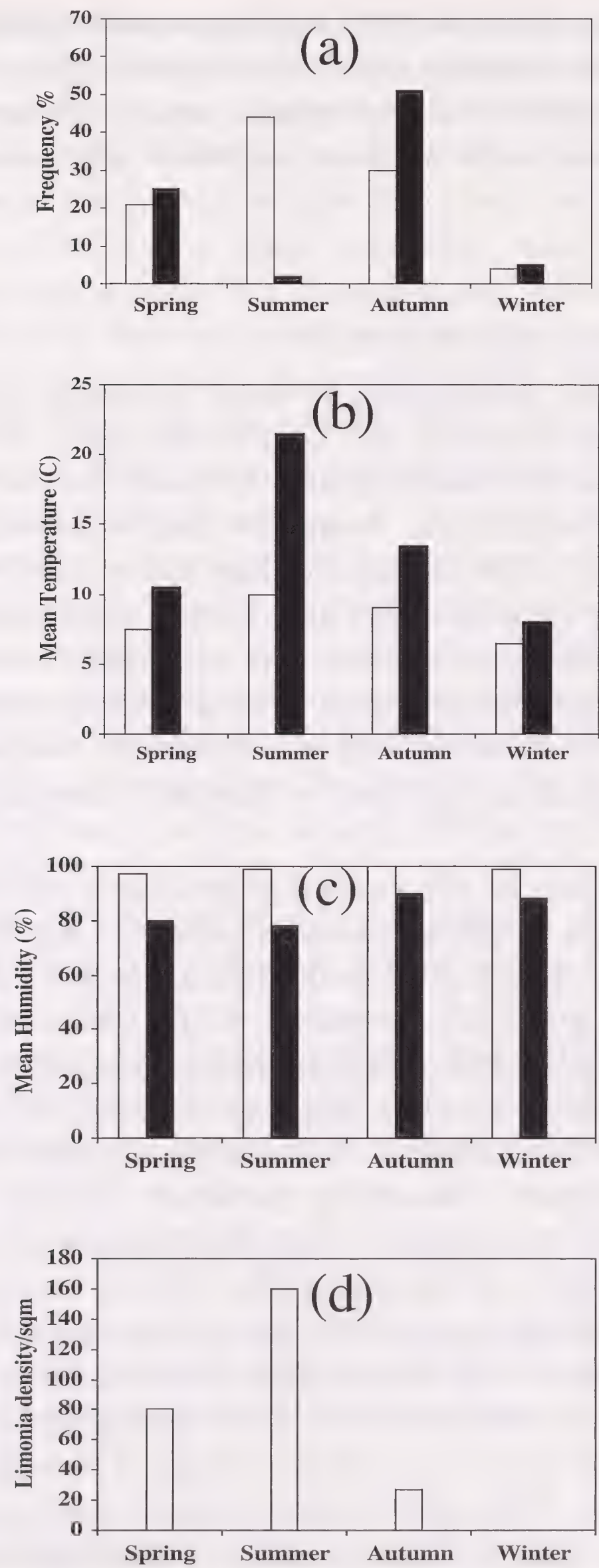


Fig. 4 - Mean values averaged per season of the following parameters recorded inside (white) and outside (black) the cave from *S. ambrosii* site 4: a) number of specimens (N_i , N_e); b) temperature (T_i , T_e); c) humidity (H_i , H_e); d) density of *Limonia* flies (N_{lim}).

entrance. Between October 1991 and September 1993, 21 specimens were observed alternatively inside and outside the cave during different surveys. Individual movements are in the order of tens of metres per month, with a mean recorded value of 0.5 (± 0.2) m/day.

DISCUSSION AND CONCLUSIONS

All the studied populations revealed a marked seasonal cycle in their surface activity inside and outside the caves. In all cases such pattern appear to be closely linked to main environmental parameters such as temperature, humidity and availability of trophic resources (tab. 2). In particular, the data show that the underground environment may be considered as a retreat, used mainly as a refuge from adverse climatic conditions. In this sense, retreats are more or less effective proportionally to their ability to preserve a relative humidity close to saturation and to provide the necessary density of invertebrate prey, as in the case of *Limonia nubeculosa*, summering in the caves.

The comparison of the studied populations revealed a tendency in the two species to show the same seasonal responses with a bi-modal frequency. The higher peaks fall in spring and autumn (figs. 1, 2, 4), indicating a direct correlation with external humidity and an inverse correlation (partial) with both the external temperature and the availability of prey inside the cave. During the dry season, the two species also seek humid retreats, in which peaks of activity may be seen in the summer, involving the whole population (N_i , figs. 1, 2, 4) and directly correlated to both the internal and external temperature and, in part, to the availability of prey within the cave (tab. 2). The exception represented by the *S. ambrosii* population inhabiting site 3, suggests that a bi-modal behavioural response may be observed also inside the caves (N_i) if the hypogean retreat is scarcely efficacious (i.e., if internal conditions do not differ significantly from the external ones). This site, in fact, presents unfavourable microclimatic conditions and is characterised by thermophilous vegetation, mainly Mediterranean maquis. The summer refuge is, moreover, a cave with a wide entrance that makes it impossible for a constant level of humidity to be maintained or for a high summer density of

flies or other invertebrates to persist within the cave. Such adverse conditions are not present in the other studied sites, all of which occur in mesic environments characterised by deciduous woods furnishing thick cover (CIMMARUTA *et al.* 1999). Also the distribution of the *Speleomantes* observed within the caves confirms the use of such habitats on the basis of their suitability, with the frequency of individuals decreasing from the entrance and following a “zoning” pattern according to environmental and trophic parameters (SALVIDIO *et alii* 1994; SALVIDIO & PASTORINO 2002; FORTI 1998; CIMMARUTA *et alii* 1999; PASTORELLI *et alii* 2001; our unpublished data).

The numerical peak observed during summer inside caves was mainly due to the high abundance of juveniles, which also represent the population component subject to seasonal influences. The numerical variations shown by adults should probably not be interpreted only as a response to seasonal environmental variations, but could also be determined by reproductive behaviour causing them to associate in high density at the beginning of the summer. This applies especially to the pregnant females, maybe due to eggs laying which is likely to begin in late autumn (DURAND 1970, 1973; SALVIDIO *et alii* 1994).

Our data on movements of single specimens showed a different frequency of individuals observed within and outside the cave in different seasons. Also, the recapture of the same specimens either inside either outside the cave confirms that salamanders perform different behavioural strategies under different environmental conditions. This confirms the existence of a single salamander population in each site, a portion of which moves daily or seasonally between the cave and the outside. Finally, our observations support the already advanced hypothesis that competitive interaction for space, to be used as a refuge, may exist between *S. strinatii* and *S. ambrosii* when in sympatry (CIMMARUTA *et alii* 1999), since these species share the same general ecological requirements.

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ABSTRACT

Two populations of *Speleomantes strinatii* and two of *S. ambrosii* have been studied between 1990 and 1997 to determine their ecological and behavioural responses related to the changes in temperature and humidity. Each studied site presented a cave and neighbouring stone walls easy to be checked for salamanders presence or absence. The number of specimens recorded and their behaviour resulted to be different in different seasons and related to the values of temperature and humidity and to the availability of prey both within and outside the caves.

The cave was used as a retreat, mainly during the summer, providing favourable values of temperature and humidity and prey availability. When external conditions were favourable (spring and autumn, mainly) a large part of the specimens (both young and adult) moved outside. If the cave is poorly efficacious as a retreat and is placed in a xeric, less suitable environment there is no difference between the activity observed within and outside, as in the case of a *S. ambrosii* population living in a site with a Mediterranean habitat and a wide-opening small cave.

RIASSUNTO

Risposte comportamentali e variazioni stagionali di parametri autoecologici in popolazioni di *Speleomantes strinatii* (Aellen, 1958) e *S. ambrosii* (Lanza, 1955) (Amphibia, Plethodontidae).

Le risposte ecologiche e comportamentali che le popolazioni di *Speleomantes* attuano in risposta ai cambiamenti di diversi parametri ambientali (soprattutto umidità e temperatura) sono state studiate dal 1990 al 1997 in due siti abitati da *S. strinatii* e in due da *S. ambrosii*. Nei quattro siti è stato rilevato un ciclo stagionale del numero di individui attivi, correlato a temperatura, umidità relativa e disponibilità di risorse trofiche, tanto nella porzione epigea che ipogea (grotta) del sito abitato.

In particolare, la parte ipogea del sito rappresenta un rifugio che viene utilizzato più frequentemente in estate per sfuggire alle condizioni stagionali avverse se

mantiene un sufficiente tenore di umidità e disponibilità di insetti predabili. Con condizioni ambientali favorevoli si assiste allo spostamento all'esterno di almeno una parte degli individui di tutte le classi d'età, con picchi di attività superficiale all'esterno in primavera e autunno. Se il rifugio ipogeo a disposizione risulta poco efficace, come nel caso della popolazione di *S. ambrosii* localizzata in un ambiente tipicamente mediterraneo, si osserva un'attività superficiale interna simile a quella esterna, con un utilizzo del rifugio meno marcato in estate e con picchi di attività primaverili e autunnali.